REASSESSMENT OF EXTINCTION PATTERNS AMONG THE LATE PLEISTOCENE MAMMALS OF SOUTH AMERICA

by Enrique P. Lessa and Richard A. Fariña

ABSTRACT. After the formation of the Isthmus of Panama, about 2·5 Ma, a massive interchange between the previously separated mammalian faunas of South and North America took place. Afterwards, during the Late Pleistocene (Lujanian Land Mammal Age)–Holocene transition (less than 10000 years BP), many of the taxa originally present in South America became extinct. Here, we report results of a statistical assessment of the relative importance of factors potentially associated with extinctions. Several factors (namely trophic niche, origin, and body size) were tested for their association with the probability of extinction, but body mass was the *only* factor found to be significantly correlated with the probability of extinction (P < 0.0001). The reduction in deviance with the inclusion of body mass was 55·7 per cent. The fate of 85·6 per cent. of the 120 Late Pleistocene mammalian genera included in the analyses was in accordance with the predictions of a logistic regression model based only on body mass. Trophic niche and origin were also considered, but turned out not to be statistically significant. We propose that the greater resilience against extinction of North American mammalian contingents played no role in the dynamics of the interchange. Also, the analyses demonstrated that marsupials did not go extinct more than placentals. Mammals of North American origin were successful invaders of the South American subcontinent because of their higher speciation rate, and not because of their lower extinction rates.

THIS study constitutes a reassessment of one aspect of the much debated Great American Biotic Interchange (GABI), specifically the hypothesis postulating a competitive displacement of native South American mammal stocks by their colonizing North American counterparts.

After the formation of the Isthmus of Panama, about 2.5 Ma, a massive interchange took place between the previously separated mammalian faunas of South and North America (Webb 1976; Marshall *et al.* 1982). Afterwards, during the Late Pleistocene (Lujanian Land Mammal Age)—Holocene transition (less than 10000 years BP), many of the native South American taxa became extinct (Simpson 1980). These phenomena and their relationships have received wide attention, but the causes of the extinctions associated with the interchange remain controversial (Owen-Smith 1987; Marshall 1988; Webb 1991). Simpson's (1950, 1980) classical hypothesis contends that the main cause of extinction was the superiority of the faunal contingents of North American origin, which would have outfought their South American counterparts in the struggle for life. This hypothesis of 'competitive displacement' has been championed by Webb (1976, 1985). Even though it has been criticized by other researchers (see below), it remains, explicitly or not, the predominant point of view.

By way of example, Gould (1980, following Parker 1977) attributed the comparative misfortune of marsupials in regard to placentals (a subject we will discuss below) not to their intrinsic lack of evolutionary advantages but to their previous evolutionary history in the relative isolation of their South American homeland. Bakker (1986, p. 443) stated that 'North American immigrants devastated the native fauna', and that 'most of the big South American species went extinct, victims of predation and competition from the northerners'. Also, Novacek (1986), in his review of Stehli and Webb (1985), stated that 'the North American components of this exchange brought havoc to much of South America's resident mammal fauna, forcing the extinctions of many lineages'. A more

prudent point of view was held by Marshall (1988), but the notion that the interaction with the North American competition-experts overwhelmed their isolation-accustomed South American counterparts pervaded the paper, in which it was euphemistically said that 'these differences in the histories...signalled the fact that aspects of the interchange would be different on each continent'.

Some authors have questioned the biological bases of the 'competitive displacement' hypothesis, indicating that the ecological equivalence of the alleged North and South American competitors is unclear and that several of the South American endemic stocks began their decline well before the arrival of North American immigrants (Patterson and Pascual 1972; Marshall and Hecht 1978; Benton 1987, 1991; Goin 1989; Ortiz Jaureguízar 1989; Pascual 1989). Unfortunately, discussions of this subject have relied primarily upon either qualitative assessments, lacking the rigour of advanced statistical tests (Stehli and Webb 1985), or analyses of pairs of allegedly equivalent groups, chosen to show a general pattern from such examples (Webb 1976, 1991; but see Marshall and Hecht 1978). We think that specific cases can only be used following the demonstration of the general patterns they mean to illustrate.

The question to be asked at this point is not really why North American contingents did better than their South American counterparts but whether and, if so, in what sense. The prevailing view taken as a whole, i.e. that North American contingents outcompeted South American ones, is difficult to assess (let alone test statistically). However, we have identified one aspect amenable to statistical testing and have adopted a suitable statistical approach. In particular, we have focused on a specific corollary from Simpson's hypothesis, which predicts an extinction bias with regard to origin among the mammals present in South American following the interchange. One variant of this hypothesis focuses instead on the differences between marsupials and placentals; while the specific reasons are debated, the superiority of placentals over marsupials has been taken almost for granted (but see Parker 1977; Gould 1980).

To test either variant of the classical viewpoint, the body sizes of the genera involved must be taken into account. Indeed, body size is widely regarded as a major factor in determining a species' susceptibility to extinction (Flessa *et al.* 1986; Pimm 1991), both in general and especially in the case under study. We presumed that neither variant would stand a statistical test after body size and other relevant factors different from origin or 'marsupialness' had been included.

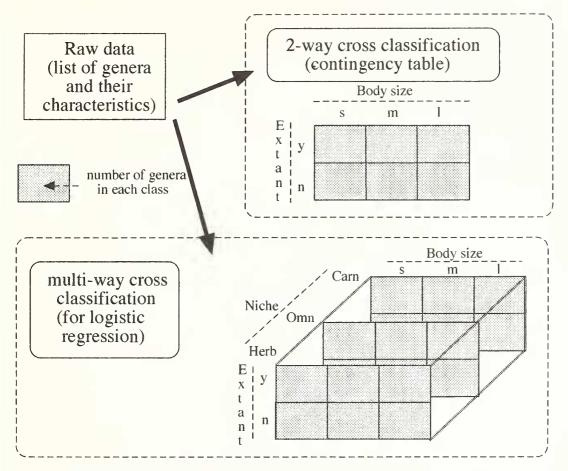
For testing these hypotheses, we adopt here a global, quantitative approach of the whole mammal fauna involved. Our analysis compares extinction rates of North and South American mammal contingents, themselves heterogeneous from a phylogenetic standpoint. The conceptual framework was developed for the macroevolutionary processes of competition among species and monophyletic taxa, but it can be readily utilized in our assessment of the relative success of these contingents. We focus here on death bias (Gould 1982) as a potential pattern favouring certain taxa at the expense of others.

MATERIAL AND METHODS

Factors and data set. We have addressed the relative predictive value and statistical significance of various factors, chosen for their presumed correlation with the probability of extinction. We took 120 of the genera listed by Marshall et al. (1984) for the Late Pleistocene (Lujanian Land Mammal Age) of South America and classified them according to the following characteristics (Appendix I):

1. Their origin, i.e. the South or North American source of the family before the beginning of the interchange in the Late Pliocene (c. 2·5 Ma). Sigmodontine rodents were classified as North American in origin. Although some scholars contend that their invasion of South America might have preceded the formation of the Isthmus of Panama (Hershkovitz 1966; Reig 1981), their classification here as of North American origin would, in any case, favour Simpson's point of view.

2. Their trophic niche, initially including six, later grouped into three, categories (carnivores, omnivores and herbivores). This reduction undoubtedly made the trophic classification relatively coarse. A more refined subdivision, as used by Patterson (1984), however, cannot yet be achieved for exclusively fossil South American mammals, because their palaeobiology has not received enough attention to permit sound hypotheses about their inferred habits.



TEXT-FIG. 1. Diagram representing the processing of data for analysis. To ask whether extinction is correlated with body size, for example, one needs a two-way cross classification summarizing how many genera of each size class are living or extinct. A χ^2 -test may be carried out using those data. An analysis attempting to assess the association of extinction with several other factors requires a multi-way classification, of which the 3-way table in the figure (bottom) is an example. s = small; m = medium; l = large; y = yes; n = no. See Appendix for other abbreviations.

3. Their mass, comprising three categories (less than 1 kg, between 1 and 100 kg, and more than 100 kg). Something must be said here about introduction of a possible size-related taphonomic bias (Damuth 1982). Although some groups of small mammals, especially the forest-dwelling primates, are not represented in the Lujanian sample, our analysis is not critically affected, because we are comparing genera living in the Lujanian, regardless of whether or not they became extinct in the Recent. Only a very different pattern of extinction among underrepresented groups could significantly change our conclusions.

A separate analysis excluded origin and replaced it by 'marsupialness,' a variable classifying taxa as either marsupials or placentals. This allowed us to test for any relevant differences between marsupials and placentals with respect to extinction.

The classification criteria outlined above are generally conservative. We preferred our data to be coarse and reliable, rather than finer and doubtful.

Statistical analysis. The first set of analyses was carried out on contingency tables cross-classifying each of the factors described above with the extinct-extant status of the genera. For each contingency table, χ^2 -tests were utilized to assess whether extinctions were independent from the factors in question. Notice that these tests take factors one at a time.

Additionally, the data were analysed by means of a stepwise, maximum likelihood logistic regression, an analogue of multiple regression suitable for dealing with qualitative response variables (McCullagh 1980; McCullagh and Nelder 1989). This procedure allows the sequential or simultaneous inclusion of factors into the model to assess their statistical significance and predictive value. These analyses were carried out by fitting logistic regression models using SAS-PC (SAS Institute 1992). The reduction in deviance after the inclusion of each factor estimates its relative importance. The models were examined for their goodness of fit.

A diagrammatic representation of our statistical approaches is presented in Text-figure 1. All analyses share the fact that they are based on cross-classification of several factors.

RESULTS

The χ^2 -tests of contingency tables suggested that, taken one at a time, all factors except origin were significantly correlated with the probability of extinction (Table 1). Unsurprisingly, body size shows the most dramatic association with extinctions, but niche and marsupialness are also significant. The latter is interesting in that marsupials appear less, not more prone to extinction than placentals.

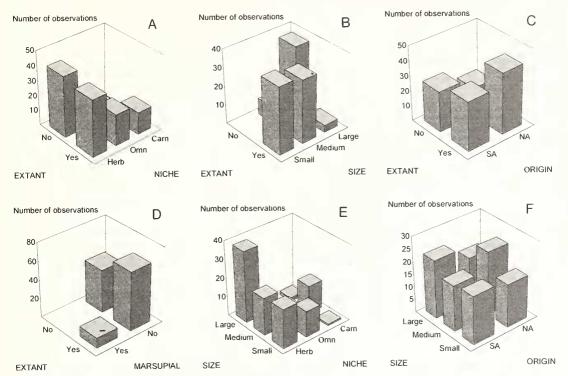
TABLE 1. Summary statistics of contingency tables testing the independence of extinction with regard to several factors.

Factor	Degrees of freedom	χ^2	P	
Body mass	2	74.625	0.001	
Niche	2	18.271	0.001	
Origin	1	2.256	0.133	
Marsupial/placental	1	7.528	0.006	

The data on which the analyses are based are depicted in Text-figure 2. Although, as just indicated, not all associations are significant, Text-figure 2 shows the following trends: (1) herbivores were more prone to extinction than omnivores or carnivores; (2) so were large animals

TABLE 2. Results of a stepwise logistic regression using origin, niche and body mass as factors to predict the probability of extinction among Late Pleistocene South American mammals.

Factor	Included in the model?	P
A. Standard data set		
Intercept	Yes	0.0001
Body mass	Yes	0.0001
Niche	No	0.1003
Origin	No	0.1318
B. Marsupial/placental factor instead of origin		
Intercept	Yes	0.0001
Body mass	Yes	0.0001
Niche	No	0.1003
Marsupial/placental	No	0.4432



TEXT-FIG. 2. Frequency histograms of several combinations of the variables examined in this study. On the left hand side niche (A), size (B), and origin (C) are examined in relation to the current status of the genera (extant or extinct). The status of marsupials and placentals are similarly examined in D. Finally, it is shown that niche and origin are correlated with size (E-F), i.e. that the categories in those factors are biased with respect to body mass. Thus, size, niche and origin are not independent from each other. See Appendix for abbreviations.

compared with smaller ones; and (3) South American residents compared with North American immigrants; as well as (4) placentals relative to marsupials.

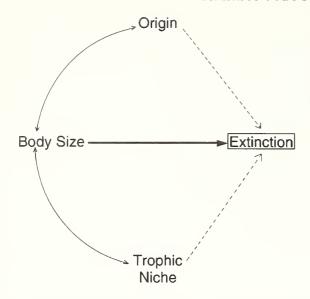
In contrast with the results of two-way contingency tables, logistic regression analyses (Table 2) indicated that only body mass was statistically significant, and very highly so (P < 0.0001). The inclusion of body mass alone reduced the deviance by 55.7 per cent. The additional inclusion of trophic niche and origin was not warranted (Table 2).

Again, the data depicted in Text-figure 2 may help understand the contrast between logistic regression, that singles out body size as the only significant factor associated with extinction, and two-way contingency tables, in which niche is significant as well. Size and niche are correlated, primarily because large animals tend to be herbivores, and both factors are significant in relation to extinction taken one at a time. Once size is included in a logistic regression, the significance of niche disappears, most probably because it indirectly reflects the importance of body size.

Replacing the factor origin with the factor 'marsupialness' did not change the situation; the hypothesis that the condition of being marsupial was not relevant to the proneness to extinction could not be rejected (P < 0.4432).

DISCUSSION AND CONCLUSIONS

It can be clearly concluded that, among the factors discussed above, body size is, as expected, overwhelming in its predictive value. In agreement with other cases of large-scale extinctions, larger South American mammals tended to become extinct significantly more often than smaller ones



TEXT-FIG. 3. Diagrammatic summary of our interpretation of the data. Only one factor (body size) accounts for the likelihood of extinction among late Pleistocene South American mammals. However, because niche and origin are correlated with body size, they may also show correlation with extinction. Such correlation disappears in logistic regressions that consider those factors simultaneously.

(Martin and Klein 1984; Benton 1990; Raup 1993). Thus, and as in other extinction events, the higher specialization that large size implies led to a differential extinction of large mammals.

This result is not surprising in itself, but suggests that considering other factors in the absence of body size data would be inappropriate. Thus, several factors showed statistical significance in the contingency tables, but such significance disappeared when those factors were considered simultaneously in a stepwise logistic regression. This indicates, firstly, that those factors are not independent of each other. As an obvious example, body mass and trophic niche are not uncorrelated in nature. Secondly, and more importantly, the statistically significant results of contingency tables for many of the factors are all heavily influenced by the hidden but pervasive influence of body mass in all analyses. Logistic regression permits identification of body mass as the only factor significantly correlated with extinction in the end of the Lujanian.

Text-figure 3 summarizes our hypothesis about the relationships between niche, origin, body mass and extinction. We propose that body mass is the only factor directly correlated with extinction because of its overriding ecological and demographic significance. Since niche and origin are correlated with body size (i.e. are biased with respect to body size), they may show indirect correlation with extinction. The statistical significance of such correlation, if present, as in the case of niche, should and does disappear when this factor is considered simultaneously with body size.

Statistical significance and causation are different matters, but it can be stated that the pattern revealed by the analyses is consistent with previously proposed processes that would primarily affect large animals, e.g. that large mammals were more vulnerable to the human *blitzkrieg* (Martin and Klein 1984), or that the large mammals were less capable of facing adverse climate changes during the Pleistocene-Holocene transition (see Marshall and Cifelli 1990 for review).

Origin, a much discussed factor presumably correlated with extinction, was not significant taken in isolation or in the context of logistic regressions (Tables 1 and 2). Mammals of South American pedigree were no more prone to die out than their North American counterparts. Contrary to theoretical expectations (Patterson 1984), trophic niche was not a significant factor in these analyses. This may be due to the overriding effect of body mass or to the inevitably coarse subdivision of niches in our data set.

The hypothesis proposing the evolutionary inferiority of marsupials was refuted, at least in connection with this particular extinction phenomenon.

Our analyses show that Simpson was not correct in his statement that mammals of North American origin were less prone to extinction than those of South American origin at the Pleistocene–Holocene boundary. However, the North American contingent did show a superiority in having higher diversification patterns after the interchange, as suggested by some authors (Marshall *et al.* 1992).

In fact, using Gould's (1982) terminology of evolution above the species level, it can be stated that the species belonging to the North American invaders were superior to the South American ones due to a birth bias, but not to a death bias in their favour. Indeed, Marshall *et al.* (1982), while establishing a higher figure of extinction rates for natives (0·5 genera per genus per million years, from Huayquerian to Recent) in comparison with immigrants (0·3 genera per genus per million years, for the same period), expressed the possibility that this could have been explained by multiple immigrations rather than by differences in the actual extinction rates. Furthermore, Cione and Tonni (1995) refined the stratigraphy of southern South America, and claimed that the arrival of mammals into that region was not as sudden as previously stated.

One possible objection to all of our analyses is that we arbitrarily emphasized the latest extinction event of what was in fact a protracted and presumably complex process of faunal dynamics. Granted, ours is a limited focus, but this results from several biological and statistical considerations.

Two points must be mentioned in this respect:

1. Earlier extinctions can be regarded as background ones, and only the one considered here is a proper mass extinction. As a matter of fact, 22 per cent. of the genera present in the Early Pleistocene (Marplatan Land Mammal Age; Cione and Tonni 1995) are not found in the Ensenadan, the following Land Mammal Age, and 7 per cent. of the Ensenadan genera are not found in the Lujanian. The percentage of the extinct Lujanian genera is 40 per cent., which qualifies for a mass extinction of intermediate level according to the criterion proposed by Sepkoski (1986) at a global scale, and is actually higher than the percentage of genera which became extinct in the Cretaceous-Tertiary boundary event. The percentages of extinction between preceding strata, in contrast, are well within values given by Raup and Sepkoski (1986) for background or minor extinctions.

2. The fortunate fact that post-Lujanian extinctions were most significant after the Great American Interchange allowed us to approach the requirements of the statistical methodologies employed in our assessment. No other comparison of strata comes closer to meeting the requirement of an unequivocal classification of all taxa to be employed with respect to the factors to be utilized. Taxonomic uncertainties are no less of a factor in our case, but we can assert that a taxon became extinct or survived the Lujanian with much greater confidence.

In conclusion, we investigated the most significant period of extinctions following the Great American Interchange, for which the quantity and quality of data happen to be the best. Earlier phases of the interchange simply fail to comply with these characteristics.

It could be argued that the displacement of the least fit South American taxa took place at an earlier phase, but then the fitter North American stocks remaining should still have been able to

outcompete their remaining native competitors.

We also carried out analyses specifically directed at alternative ways of classifying some of the taxa in our data. For instance, one of us (Fariña in press) claimed, on palaeoecological grounds, that ground sloths could have been opportunistic flesh eaters. The analysis was run with the due change in the data, i.e. ground sloths were taken as omnivorous, but the results were very similar. The niche was again non-significant as a factor explaining extinction, and, more generally, results did not change substantially for the factors considered. Another potential source of bias in the results was the fact that sigmodontine cricetids were considered as having a North American origin, but, again, the changes in the figures yielded by the analysis classifying them as South American were only minor. Finally, we conducted a separate logistic regression on the basis of the genera listed by Tonni *et al.* (1992) for the Pampean region, by far the best documented Late Pleistocene fauna of South America, and, once more, body mass turned out to be the only significant factor associated with extinction. In sum, the alternatives tested so far do not change our fundamental results.

The analytical power of logistic regression and related statistical tools is well illustrated by our analyses. Such tools will be useful in future studies of the causes of extinction, such as the differences

in extinction rates between mammals of open country and forested habitats (Vrba 1992). Additionally, progress on the issue of extinction patterns will require further refinement of the categories utilized in the data analysis.

The invasion by North American mammal contingents had a dramatic impact upon the faunal composition of South America. Differential extinction of both stocks, however, cannot account for such an effect, the causes of which must be sought elsewhere (for reviews of various proposals, see Martin and Klein 1984; Marshall and Cifelli 1990; Webb 1991).

On the other hand, North American invaders were very successful in doing precisely that, i.e. invading. Pimm (1991) analysed the difficulties faced by any species invading a new habitat. Many species belonging to the North America mammal fauna succeeded in this task when a land bridge was available, and even before. Moreover, once established, they speciated much more than the endemics, and hence their number grew exponentially (Webb and Marshall 1982).

Unfortunately, other factors involved in faunal dynamics, such as differential speciation, cannot be tested as easily, since logistic regression requires a reliable and complete cross-classification of all taxa for all factors.

Acknowledgements. We are grateful to D. Brillinger, E. Ganón and C. Gutiérrez for statistical advice, and to M. J. Benton, M. Juanicó, B. D. Patterson, J. L. Patton, D. B. Wake, S. D. Webb and one anonymous referee for comments on earlier versions of the text.

REFERENCES

BAKKER, R. T. 1986. The dinosaur heresies. Morrow, New York, 481 pp.

BENTON, M. J. 1987. Progress and competition in macroevolution. Biological Reviews, 62, 305-338.

—— 1990. Evolution of large size. 147–152. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds)., *Palaeobiology: a synthesis*. Blackwell, Oxford, 583 pp.

—— 1991. Extinction, biotic replacements, and clade interactions. 89–102. *In DUDLEY*, E. C. (ed.). *The unity of evolutionary biology*. Dioscorides Press, Portland, 1160 pp.

CIONE, A. L. and TONNI, E. P. 1995. Chronostratigraphy and 'Land-Mammal Ages' in the Cenozoic of Southern South America: principles, practices, and the 'Uquian' problem. *Journal of Paleontology*, **69**, 135–159.

DAMUTH, J. 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology, 8, 434–446.

FARIÑA, R. A. in press. Trophic relationships among Lujanian mammals. Evolutionary Theory.

FLESSA, K. W. and 11 others. 1986. Causes and consequences of extinctions. 235–257. In RAUP, D. M. and JABLONSKI, D. (eds). Patterns and processes in the history of life. Springer Verlag, Berlin, 447 pp.

GOIN, F. J. 1989. Late Cenozoic South American marsupial and placental carnivores: changes in predator-prey evolution. *Abstracts of Papers and Posters*, 5th International Theriological Congress, Rome, vol. 1, 271–272. GOULD, S. J. 1980. Sticking up for marsupials. 289–295. In GOULD, S. J. The panda's thumb. W. W. Norton, New

York, 343 pp.

—— 1982. The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution. 83–104. *In MILKMAN, R. (ed.). Perspectives on evolution.* Sinauer, Sunderland, 242 pp.

HERSHKOVITZ, P. 1966. The recent mammals of the Neotropical region: a zoogeographic and ecological review. 725–747. *In* WENZEL, R. L. and TIPTON, V. J. (eds). *Ectoparasites of Panama*. Field Museum of Natural History, Chicago, 861 pp.

MARSHALL, L. G. 1988. Land mammals and the Great American Interchange. *American Scientist*, **96**, 380–388. ——BERTA, A., HOFFSTETTER, R., PASCUAL, R., REIG, O. A., BOMBÍN, M. and MONES, A. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata*, *Mémoire Extraordinaire*, **1984**, 1–76.

— and CIFELLI, R. L. 1990. Analysis of changing diversity patterns in Cenozoic band mammal age fauna, South America. *Palaeovertebrata*, 19, 169–210.

— and HECHT, M. K. 1978. Mammalian faunal dynamics of the Great American Interchange: an alternative interpretation. *Paleobiology*, 4, 203–209.

- Webb, S. D., Sepkoski, J. J., Jr and RAUP, D. M. 1982. Mammalian evolution and the great American interchange. *Science*, **215**, 1351–1357.
- MARTIN, P. S. and KLEIN, R. G. 1984. *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson, 891 pp.
- McCullagh, P. 1980. Regression models for ordinal data (with discussion). *Journal of the Royal Statistical Society*, **42**, 109–142.
- and NELDER, J. A. 1989. Generalized linear models. Chapman and Hall, London, 505 pp.
- NOVACEK, M. J. 1986. A biogeographic event. Science, 231, 1021-1022.
- ORTIZ JAUREGUÍZAR, E. 1989. Analysis of the compositional changes of the South American mammal fauna during the Miocene–Pliocene (Panaraucanian faunistic cycle). Abstract of Papers and Posters, 5th International Theriological Congress, Rome, vol. 1, 277–278.
- OWEN-SMITH, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 13, 351–362. PARKER, P. 1977. An ecological comparison between marsupial and placental patterns of reproduction.
- 273–286. In Stonehouse, B. and GILMORE, D. (eds). The biology of marsupials. Macmillan, London, 486 pp. PASCUAL, R. 1989. Late Cenozoic mammal dispersal between the Americas: an overview of the South American evidences. Abstract of Papers and Posters, 5th International Theriological Congress, Rome, vol. 1, 279–280.
- PATTERSON, B. and PASCUAL, R. 1972. The fossil mammal fauna of South America. 247–309. *In* KEAST, A., ERK, F. C. and GLASS, B. (eds). *Evolution, mammals and southern continents*. State University of New York Press, Albany, 543 pp.
- PATTERSON, B. D. 1984. Mammalian extinction and biogeography in the Southern Rocky Mountains. 247–293. In NITECKI, M. H. (ed.) Extinctions. University of Chicago Press, Chicago, 354 pp.
- PIMM, S. L. 1991. Balance of Nature? Ecological issues in the conservation of species and communities. University of Chicago Press, Chicago, 434 pp.
- RAUP, D. M. 1993. Extinction: bad genes or bad luck? Oxford University Press, Oxford, 216 pp.
- and SEPKOSKI, J. J., Jr 1986. Periodic extinction of families and genera. Science, 231, 833–836.
- REIG, O. A. 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. *Monographiae Naturae*, 1, 1–162.
- SAS 1992. Statistical Analysis System. Version 6.1. SAS Institute, Cary, 846 pp.
- SEPKOSKI, J. J., Jr 1986. Global bioevents and the question of periodicity. 47–61. *In* WALLISER, O. (ed.). *Global bio-events*. Springer Verlag, Berlin, 442 pp.
- SIMPSON, G. G. 1950. History of the fauna of Latin America. American Journal of Science, 38, 361-389.
- —— 1980. Splendid isolation, the curious history of South American mammals. Yale University Press, New Haven, 266 pp.
- STEHLI, F. G. and WEBB, S. D. (eds). 1985. *The Great American Biotic Interchange*. Plenum, New York, 532 pp. TONNI, E. P., ALBERDI, M. T., PRADO, J. L., BARGO, M. S. and CIONE, A. L. 1992. Changes of mammal assemblages in the Pampean region and their relation with the Plio-Pleistocene boundary. *Palaeogeography*, *Palaeoclimatology*, *Palaeocology*, 95, 179–194.
- VRBA, E. 1992. Mammals as a key to evolutionary theory. Journal of Mammalogy, 73, 1–28.
- WEBB, S. D. 1976. Mammalian faunal dynamics of the Great American interchange. *Paleobiology*, **2**, 216–234. ——1985. Late Cenozoic mammal dispersals between the Americas. 357–386. *In* STEHLI, F. G. and WEBB, S. D. (eds). *The Great American Biotic Interchange*. Plenum, New York, 532 pp.
- —— 1991. Ecogeography and the great American biotic interchange. *Paleobiology*, 17, 266–280.
- and Marshall, L. G. 1982. Historical biogeography of recent South American land mammals. *In Mares*, M. A. and Genoways, H. H. (eds). *Mammalian biology in South America*. Pymatuning Symposia on Ecology, Special Publication Series, 6, 39–52.

ENRIQUE P. LESSA

Laboratorio de Evolución Facultad de Ciencias Tristán Narvaja 1674 Montevideo 11200, Uruguay

RICHARD A. FARIÑA
PEDECIBA Biología
Facultad de Ciencias
Tristán Narvaja 1674
Montevideo 11200, Uruguay

Typescript received 16 January 1995 Revised typescript received 8 October 1995

APPENDIX

List of genera considered in the analysis. Their origin has been classified as either South or North American, their trophic niche as herbivore, omnivore or carnivore, and their size as small, medium or large, according to the criteria discussed in the text. * = marsupials; NA = North American; SA = South American; Carn = carnivorous; Herb = herbivorous; Omn = omnivorous.

Genus	Extant	Origin	Niche	Size
1 Caluromys*	Yes	SA	Omn	Small
2 Chironectes*	Yes	SA	Omn	Small
3 Didelphis*	Yes	SA	Omn	Medium
4 Lestodelpliys*	Yes	SA	Omn	Small
5 Lutreolina*	Yes	SA	Omn	Small
6 Marmosa*	Yes	SA	Omn	Small
7 Micoureus*	Yes	SA	Omn	Small
8 Metachirus*	Yes	SA	Omn	Medium
9 Monodelphis*	Yes	SA	Omn	Small
10 Philander*	Yes	SA	Omn	Small
11 Thylamys*	Yes	SA	Omn	Small
12 Cryptotis	Yes	NA	Omn	Small
13 Cabassous	Yes	SA	Omn	Medium
14 Chaetophractus	Yes	SA	Omn	Medium
15 Chlamyphorus	Yes	SA	Omn	Small
16 Dasypus	Yes	SA	Omn	Medium
17 Euphractus	Yes	SA	Omn	Medium
18 Eutatus	No	SA	Herb	Medium
19 Pampatherium	No	SA	Herb	Large
20 Propraopus	No	SA	Omn	Medium
21 Tolypeutes	Yes	SA	Herb	Medium
22 Zaedyus	Yes	SA	Omn	Medium
23 Chlamydotherium	No	SA	Herb	Large
24 Doedicurus	No	SA	Herb	Large
25 Glyptodon	No	SA	Herb	Large
26 Hoplophorus	No	SA	Herb	Large
27 Neothoracophorus	No	SA	Herb	Large
28 Panochthus	No	SA	Herb	Large
29 Plaxhaplous	No	SA	Herb	Large
30 Sclerocalyptus	No	SA	Herb	Large
31 Nothropus	No	SA	Herb	Medium
32 Nothrotherium	No	SA	Herb	Large
33 Ocnopus	No	SA	Herb	Large
34 Valgipes	No	SA	Herb	Medium
35 Eremotherium	No	SA	Herb	Large
36 Megatherium	No	SA	Herb	Large
37 Glossotherium	No	SA	Herb	Large
38 Lestodon	No	SA	Herb	Large
39 Mylodon	No	SA	Herb	Large
40 Scelidodon	No	SA	Herb	Large
41 Scelidotherium	No	SA	Herb	Large
42 Sylvilagus	Yes	NA	Herb	Medium
43 Akodon	Yes	NA	Herb	Small
44 Andinomys	Yes	NA	Herb	Small
45 Auliscomys	Yes	NA	Herb	Small
46 Bolomys	Yes	NA	Omn	Small
47 Calomys	Yes	NA	Herb	Small

Gen	us	Extant	Origin	Niche	Size
48	Eligmodontia	Yes	NA	Herb	Small
	Euneomys	Yes	NA	Herb	Small
	Graomys	Yes	NA	Herb	Small
	Holochilus	Yes	NA	Herb	Small
	Kunsia	Yes	NA	Herb	Small
	Nectomys	Yes	NA	Herb	Small
	Oxymycterus	Yes	NA	Omn	Small
	Phyllotis	Yes	NA	Herb	Small
	Reithrodon	Yes	NA	Herb	Small
	Scapteromys	Yes	NA	Omn	Small
	Ctenomys	Yes	SA	Herb	Small
	Abrocoma	Yes	SA	Herb	Small
	Carterodon	Yes	SA	Herb	Small
	Euryzygomatoniys	Yes	SA	Herb	Small
	Proechiniys	Yes	SA	Herb	Small
	Thrichonys	Yes	SA	Herb	Small
	Myocastor	Yes	SA	Herb	Medium
	Lagostomus	Yes	SA	Herb	Medium
	Lagidium	Yes	SA	Herb	Medium
	Coendou	Yes	SA	Herb	Medium
	Cavia	Yes	SA	Herb	Small
	Dolichotis	Yes	SA	Herb	Medium
	Galea	Yes	SA	Herb	Small
	Microcavia	Yes	SA	Herb	Small
	Hydrochoerus	Yes	SA	Herb	Medium
	Neochoerus	No	SA	Herb	Large
	Canis	Yes	NA	Carn	Medium
	Cerdocyon	Yes	NA	Carn	Medium
	Clirysocyon	Yes	NA	Carn	Medium
	Dusicyon	Yes	NA	Carn	Medium
	Lycalopex	Yes	NA	Carn	Medium
	Protocyon	No	NA	Carn	Medium
	Speothos	Yes	NA	Carn	Medium
	Theriodictis	No	NA	Carn	Medium
	Arctodus	No	NA	Omn	Large
	Nasua	Yes	NA	Carn	Medium
	Conepatus	Yes	NA	Carn	Medium
	Galera	Yes	NA	Carn	Medium
	Galictis	Yes	NA	Carn	Medium
	Lyncodon	Yes	NA	Carn	Medium
	Lutra	Yes	NA	Carn	Medium
	Mustela	Yes	NA	Carn	Small
	Felis	Yes	NA	Carn	Medium
	Leo	Yes	NA	Carn	Large
	Smilodon	No	NA	Carn	Large
	Macrauchenia	No	SA	Herb	Large
	Windhausenia	No	SA	Herb	Large
	Mixotoxodon	No	SA	Herb	Large
	Toxodon	No	SA	Herb	Large
	Cuvieronius	No	NA	Herb	Large
	Haplomastodon	No	NA	Herb	Large
	Natiomastodon	No	NA	Herb	Large

Genus	Extant	Origin	Niche	Size
100 Stegomastodon	No	NA	Herb	Large
101 Equus	No	NA	Herb	Large
102 Hippidion	No	NA	Herb	Large
103 Onohippidion	No	NA	Herb	Large
104 Tapirus	Yes	NA	Herb	Large
105 Brasiliochoerus	No	NA	Herb	Medium
106 Catagonus	Yes	NA	Herb	Medium
107 Tayassu	Yes	NA	Herb	Medium
108 Platygonus	No	NA	Herb	Large
109 Eulamaops	No	NA	Herb	Large
110 Lama	Yes	NA	Herb	Large
111 Palaeolama	No	NA	Herb	Large
112 Agalmaceros	No	NA	Herb	Large
113 Blastocerus	Yes	NA	Herb	Large
114 Hippocamelus	Yes	NA	Herb	Medium
115 Mazama	Yes	NA	Herb	Medium
116 Morenelaphus	No	NA	Herb	Medium
117 Odocoileus	Yes	NA	Herb	Medium
118 Ozotoceros	Yes	NA	Herb	Medium
119 Paraceros	No	NA	Herb	Medium
120 Antifer	No	NA	Herb	Large